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Current Status and Future Perspectives on Distribution of Fungal Endophytes and Their Utilization for Plant Growth Promotion and Management of Grapevine Diseases

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Abstract

Grapevine is one of the economically most important fruit crops cultivated worldwide. Grape production is significantly affected by biotic constraints leading to heavy crop losses. Changing climatic conditions leading to widespread occurrence of different foliar diseases in grapevine. Chemical products are used for managing these diseases through preventive and curative application in the vineyard. High disease pressure and indiscriminate use of chemicals leading to residue in the final harvest and resistance development in phytopathogens. To mitigate these challenges, the adoption of potential biocontrol control agents is necessary. Moreover, multifaceted benefits of endophytes made them eco-friendly, and environmentally safe approach. The genetic composition, physiological conditions, and ecology of their host plant have an impact on their dispersion patterns and population diversity. Worldwide, a total of more than 164 fungal endophytes (FEs) have been characterized originating from different tissues, varieties, crop growth stages, and geographical regions of grapevine. These diverse FEs have been used extensively for management of different phytopathogens globally. The FEs produce secondary metabolites, lytic enzymes, and organic compounds which are known to possess antimicrobial and antifungal properties. The aim of this review was to understand diversity, distribution, host–pathogen-endophyte interaction, role of endophytes in disease management and for enhanced, and quality production.

Introduction

Grapevine (*Vitis vinifera* L.) belonging to order Vitales, family Vitaceae and genus *Vitis*. Cultivation of grapes has been originated in Southern Caucasia, presently a part of northwestern Turkey, northern Iraq, Azerbaijan, and Georgia [1]. Initially, Romans were well known for categorizing grape varieties based on colour, ripening characteristics, and suitable soil types [2]. Europe and Central Asia are the major grape-growing continents. The American and Asian grape species i.e., *Vitis amurensis* Rupr. (Order: Vitales, family: Vitaceae and genus: *Vitis*) was used mainly for table and wine purposes. North American grapevine species i.e., *Vitis labrusca* L. (order: Vitales, family: Vitaceae and genus: *Vitis*) used for development of table and juice varieties. Mustang grapes (*Vitis mustangensis* Buckley) were found in Mississippi, Alabama, Louisiana, Texas, and Oklahoma for making wine and jam. Similarly, in North America, the wild species i.e., *Vitis riparia* Michx. is used. In the southeast of the United States, from Delaware to the Gulf of Mexico, *Vitis rotundifolia* Michx. or Muscadine (subgenus: *Vitis subg. Muscadinia*) is grown for their use in making jam and wine [3].

In India, grape is one of the most important fruit crops cultivated in sub-tropical and tropical, regions, covering an area of 1,61,910 hectares, accounting for 2.3% of the total fruit production area. India is also a major exporter of fresh grapes to many countries of the world; it has exported around 267,950.39 MT of grapes to the world for worth of 313.70 million USD during the year 2022–23 [4]. Of the total production in India, 80% is consumed and cultivated for table purpose, whereas 2.5% of the total production are exported to the Middle East and European countries [5]. Among the tropical countries India, Brazil, and Thailand are contributing a major share in production with respect to the world's total production [6].

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Grape cultivation is becoming more challenging due to the occurrence of several fungal, bacterial, viral, phytoplasma and viroid diseases worldwide leading to huge financial crop losses. Downy and powdery mildews, anthracnose, bacterial blight and rust are the major diseases affecting grapevine production and productivity [7–9]. To manage these diseases, continuous application of chemicals playing a major role which leading to the development of resistance in the pathogens, residues in the final harvest, human and environmental hazards. To mitigate these challenges, use of potential resident microbes with multifaceted effects needs to be explored. Biological control is an important approach of integrated disease management in grapevine in India. Use of endophytic microorganisms are reservoirs of bio-resources having array of potential roles of benefiting the host plants. The fungal endophytes (FEs) live intercellularly or intracellularly within the host tissues for the partial or complete life cycle of the plants [10]. These FEs act as potential biocontrol agents (BCAs) by protecting their host from different diseases [11]. The FEs can produce secondary metabolites that promotes plant growth, induces systemic resistance to the host, protecting host from pathogen attack, and eventually improving crop yield [12]. The FEs uses different mechanisms for the management of various diseases through direct and indirect inhibitions. Direct inhibition involves the production of several lytic enzymes such as β-1,3-glucanases, chitinases, and cellulases which hydrolyzes the cell wall of pathogens. Moreover, FEs produces several antibiotics viz., terpenoids, alkaloids, aromatic compounds, and polypeptides which are also helpful against various pathogens [13, 14].

Previously documented information on FEs viz., *Acremonium byssoides* [15], *Alternaria alternata* [16–18], *Epicoccum nigrum* [19], *Fusarium proliferatum* [20], *Trichoderma* spp. [21–23] had been designated as potential BCAs against *Plasmopara viticola* known to cause downy mildew in grapevine. Likewise, the other FEs viz., *Acremonium cephalosporium* [24], *Aphanocladium album* [25], *Epicoccum nigrum* [26], *Gliocladium* spp. [26] had been found efficient for inhibiting the growth of *Botrytis cinerea* causing grey mould in grapevine. Likewise, *Beauveria bassiana* an endophytic strain was identified for plant growth promotion in grapevine [27]. Globally, least information is available on the use of FEs as potential antagonistic microbes against *C. gloeosporioides*. Recently, Holkar et al. [28] from India, isolated 51 FEs from leaf segments of ten grapevine varieties which were belonged to *Alternaria*, *Aspergillus*, *Bipolaris, Curvularia*, *Daldinia*, *Exserohilum, Fusarium* and *Nigrospora* species. The in vitro direct confrontation assay against *C. gloeosporioides* revealed that 70%-78.94% growth inhibition was observed due to FEs isolates. Additionally, S5 and MM4 FEs were found to produce azulene and 1,3-Cyclopentanedione, 4,4-dimethyl as antimicrobial volatile organic compounds (VOCs), respectively [28]. This information is certainly helpful in devising bio-intensive disease management strategy in grapevine using endophytic microorganisms. In India, scanty information is available on the use of endophytic fungi for management of grapevine diseases [29–32].

This review aims to highlight distribution, transmission, diversity of FEs and their role in grapevine disease management and plant growth promotion. Till date, large number of research findings on antimicrobial potential of FEs against phytopathogens were carried out under *in-vitro* conditions, but their evaluations under greenhouse and field conditions is required. The FEs in grapevine is much more explored worldwide and successfully used for management of grapevine fungal diseases. However, least information is available on FEs isolated and characterized from Indian subcontinents. This review emphasises the application of FEs as potential biocontrol agents plays a pivotal role in grapevine quality production.

Effect of Abiotic and Biotic Stresses in Grapes

Grapevine has been exposed to extreme climatic conditions and, therefore, becomes vulnerable to various biotic and abiotic stresses [33]. Among the biotic stresses, phytopathogenic fungi, bacteria, viruses, nematodes, viroid, phytoplasma and different pests are the major constraints in grapevine cultivation worldwide [34, 35]. The most common and economically important fungal diseases of grapes are powdery and downy mildews, and grey mould [7, 8], anthracnose [9] and other postharvest diseases [36]. Bacterial diseases such as bacterial blight (*Xanthomonas ampelinus* and *X. campestris* pv. *viticola*), Pierce's disease (*Xylella. fastidiosa* subsp. *fastidiosa*), and crown gall (*Agrobacterium vitis*) affecting the vascular system of the vine [37]. For fungal and bacterial diseases, most of the grape varieties are lacking durable resistance and make growers dependent on hazardous chemicals. Heavy and continuous use of synthetic chemicals affects human health, the environment, and also soil microbiota [38]. Moreover, the use of toxic chemicals leading to resistance development in different phytopathogenic fungi and bacteria [39]. In addition to this, pesticides can contaminate soil, water, grasses, and other cropping systems and kill beneficial insects and other vertebrates including birds, fishes, and non-targeted plants [40].

Therefore, for safe, eco-friendly, and high-quality grape production, potential biological control agents (BCAs) offer an effective option for the chemical control of different diseases in grapes. BCAs play an important role in crop health improvement and the suppression of plant pathogens [41]. Fungal endophytes (FEs) are the hidden treasure of bio-resource having with huge diversity and immense potential to facilitate different biocontrol and growth-promotion activities [42–44].

An Overview of Fungal Endophytes

In 1866, Anton De Bary was the first scientist to propose the concept of "Endophytes" in agriculture [45]. The FEs are endosymbiont that grows inter or intracellularly by means of local and systemic distribution in the host plants without inducing any disease symptoms or affecting plant health [46–48]. Every single part of the plant harbours endophytes and their diversity depending on host plant species, tissue type, growth conditions, geographical location, and interaction with other microbes present in soil [42, 43, 49–52]. The FEs have two major groups that have been recognized previously, reflecting differences in evolutionary relatedness, taxonomy, plant hosts, and ecological functions that is clavicipitaceous endophytes, are transmitted vertically from plants to their offspring through seeds [53] and the non-clavicipitaceous endophytes transmit horizontally and vertically [54]. Non-clavicipitaceous fungi are highly distributed in different ecosystems with high-potential applications [55] (Fig. 1).

Endophytic fungi act as biocontrol agents [56], plant growth promoters, bioremediation potential boosters [57], produce novel secondary metabolites [58] and enzymes [59]. The FEs are rich in sources of bioactive compounds which have been received a considerable attention in the field of agriculture and pharmaceutical industries for commercial production. FEs are part of the plant microsystem and have been observed to promote plant growth by enhancing hormone production, such as auxin and cytokinin, which support their nutrient uptake by solubilization [60]. Additionally, they defend plants from diseases by releasing antagonistic substances, triggering host defense mechanisms, or competing for nutrients, food, and colonization sites [60].

Diversity and Distribution of Fungal Endophytes in Grapevine

The diversity and composition of the microbiota changes depending on the host plant's physiology, biochemistry, and biotic and abiotic factors. The overall composition and community of endophytes can be affected by the type of tissue analyzed [61, 62], cultivar [63, 64], plant age [65, 66], genotype [67], physiological state of the vine [68], sample collection [69] and pest management [70]. For instance, geographical and seasonal variations are reported to have high effect on the species richness, diversity, and differences [71–73]. Comparison between geographical areas showed more endophytic diversity in tropical areas than in temperate regions [55]. Distribution profile of FEs of grapevine have been reported from many parts of Asia and Europe, North America and South America (Fig. 2, Fig. 3). Different studies have shown small variations in the taxa obtained from the same plant species [74, 75].

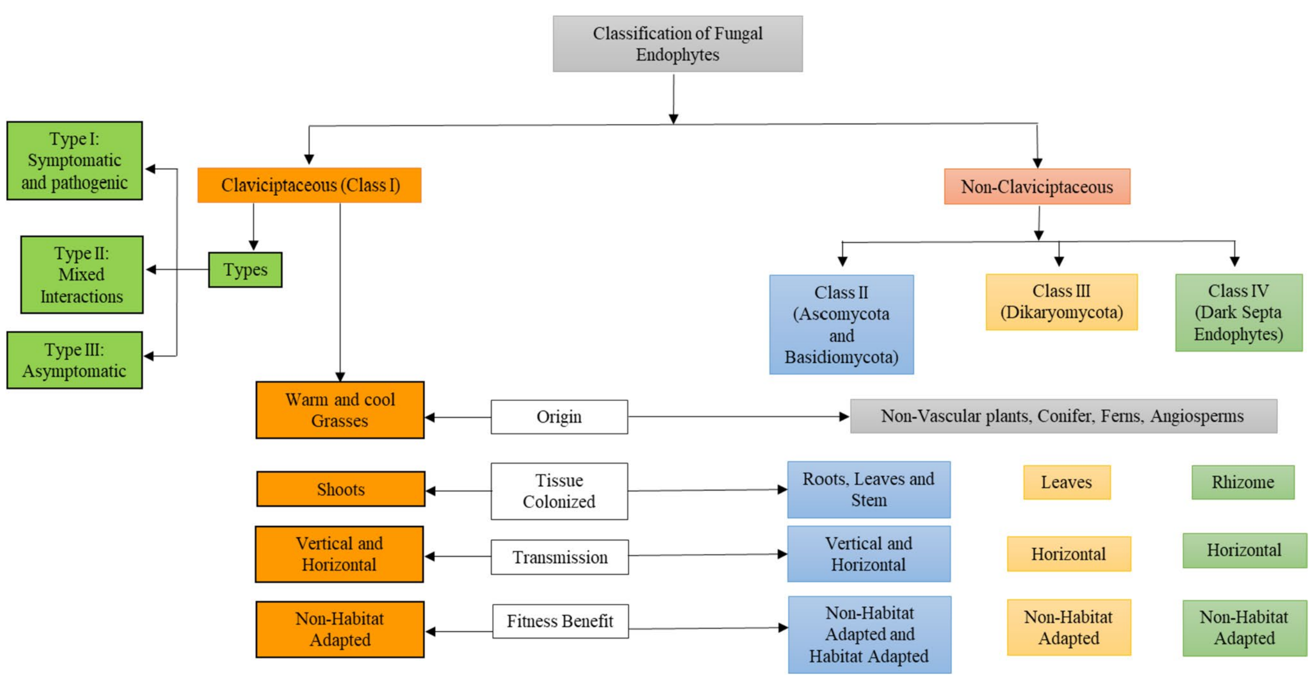

Fig. 1 Schematic representation of the classification of fungal endophytes based on interactions, origin, colonization, transmission, and fitness benefits in plants

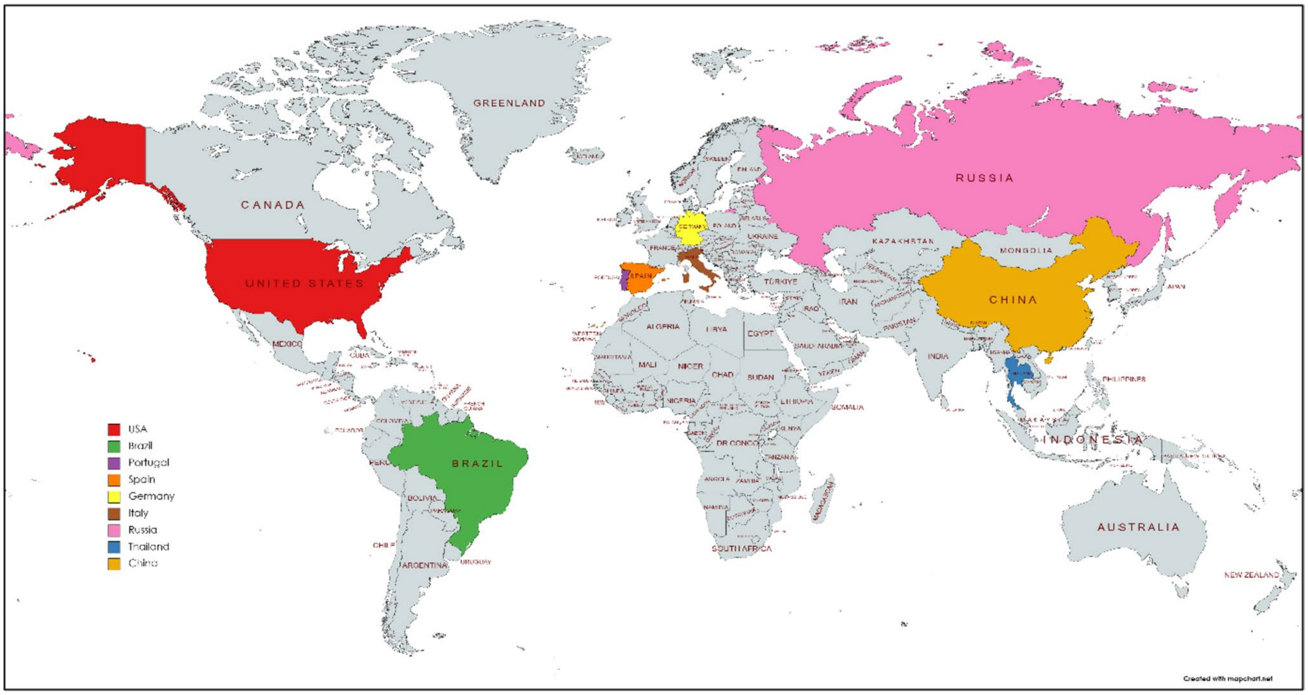

Fig. 2 Geographical distribution of fungal endophytes isolated from grapevine from different countries worldwide

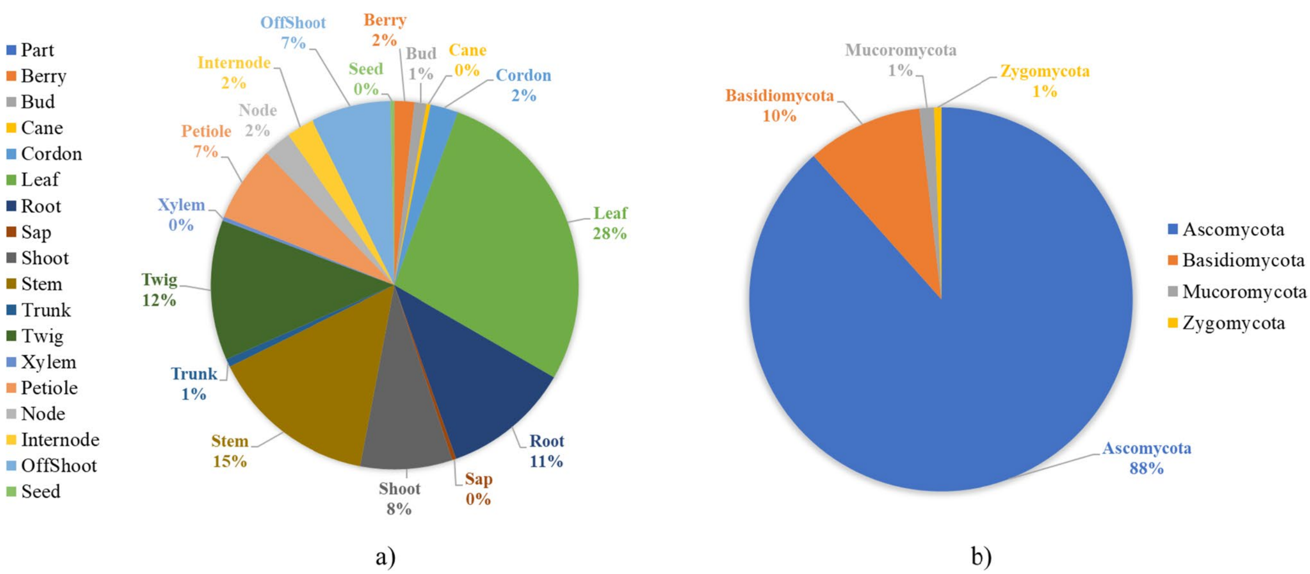

Fig. 3 Percent share of fungal endophytes isolated from different tissues of grapevine and across fungal divisions of their taxonomy

Average temperature, latitude, or annual rainfall, which are associated with geography, might influence the diversity of FEs [55]. The diversity and distribution of distinct culturable and non-culturable fungal endophytes in diverse tissues of various grapevine varieties in different countries worldwide have been documented (Tables 1 and 2).

Certain nutrients, salts, and secondary metabolites as well as each taxon's capacity to permeate distinct grape tissues, are likely to play an important role in the occurrence of fungal taxa in particular grapevine organs but this presumption needs further research [76]. Culturable FEs are isolated using different types of growth-specific media and

Table 1 Geographical and tissue-specific distribution of fungal endophytes originating from grapevines genotypes cultivated worldwide

Sl. No	Fungal Endophyte	Host Part	Grape variety	Location	Division	References
1.	*Acremonium alternatum*	Stem	Midnight beauty	East Asia	Ascomycota	[80]
2.	*Acremonium byssoides*	Leaf	Regina Bianca, Catarratto and Insolia	Europe	Ascomycota	[15]
3.	*Acremonium persicinum*	Leaf, Bud	Inzolia	Europe	Ascomycota	[78]
4.	*Acremonium sclerotigenum*	Shoot, Petiole, Bud, Seed	Inzolia	Europe	Ascomycota	[78]
5.	*Acremonium* sp.	Root, Stem, Xylem, Leaf, Twig	Tempranillo, Moscatel Grano Menudo, Malvar, Syrah, Merlot, Garnacha, Albillo, Airen, Cabernet Sauvignon; Corvina and Corvinone	Europe, South America	Ascomycota	[96, 122]
6.	*Acremonium strictum*	Twig, Leaf	Tempranillo, Moscatel Grano Menudo, Malvar, Syrah, Merlot, arnacha, Albillo, Airen, Cabernet Sauvignon; Negramoll	South America, Europe	Ascomycota	[96, 123]
7.	*Albifimbria verrucaria*	Leaf	*Vitis amurensis*	East Asia	Ascomycota	[102]
8.	*Alternaria alternata*	Twig, Shoot, Leaf, Root	*Vitis vinifera*; Tempranillo, Moscatel Grano Menudo, Malvar, Syrah, Merlot, Garnacha, Albillo, Airen, Cabernet Sauvignon; Moscatel, Tempranillo; Midnight beauty; Rose honey; *Vitis amurensis*; Trincadeira and Alicante Bouschet	East Asia, Africa, North America, Europe, Europe	Ascomycota	[16, 80, 96, 102, 104, 109, 117]
9.	*Alternaria arborescens*	Leaf, Twig, Shoot	Tempranillo, Moscatel Grano Menudo, Malvar, Syrah, Merlot, Garnacha, Albillo, Airen, Cabernet Sauvignon; Rose honey	East Asia, Europe	Ascomycota	[96, 117]
10.	*Alternaria* sp.	Twig, Shoot, Leaf, Root, Berry, Node, Internode	Tokai and Merlot; Tempranillo, Moscatel Grano Menudo, Malvar, Syrah, Merlot, Garnacha, Albillo, Airen, Cabernet Sauvignon; Chardonnay and Merlot; Negramoll and Verdelho; Rose honey; Flame, Autumn Royal, Sweet Scarlet; Trincadeira and Alicante Bouschet	Europe, North America, East Asia	Ascomycota	[64, 84, 96, 104, 77, 117, 123]

Table 1 (continued)

Sl. No	Fungal Endophyte	Host Part	Grape variety	Location	Division	References
11.	*Alternaria tenuissima*	Leaf, Shoot	Tempranillo, Moscatel Grano Menudo, Malvar, Syrah, Merlot, Garnacha, Albillo, Airen, Cabernet Sauvignon; Negramoll	Europe, East Asia, Europe	Ascomycota	[96, 109]
12.	*Ampelomyces humuli*	Stem	Chardonnay and Merlot	Europe	Ascomycota	[64]
13.	*Aporospora terricola*	Leaf	*V. labrusca* cv. 'Niagara Rosada'	South America	Ascomycota	[105]
14.	*Arthrinium rasikravindrii*	Stem	Midnight beauty	East Asia	Ascomycota	[80]
16.	*Aspergillus japonicus*	Stem	Midnight beauty	East Asia	Ascomycota	[80]
17.	*Aspergillus niger*	Twig, Shoot, Leaf, Root, Petiole, Offshoot	Midnight beauty, Tempranillo, Moscatel Grano Menudo, Malvar, Syrah, Merlot, Garnacha, Albillo, Airen, Cabernet Sauvignon; Chardonnay and Merlot; Albillo, Almuneco, Baboso Negro, Moscatel, Listan Negro, and Verdelho; Midnight; Trincadeira and Alicante Bouschet	Europe, Asia	Ascomycota	[80, 96, 104, 120]
18.	*Aspergillus pseudodeflectus*	Stem	Midnight beauty	East Asia	Ascomycota	[80]
19.	*Aspergillus pseudoglaucus*	Stem	Midnight beauty	East Asia	Ascomycota	[80]
20.	*Aspergillus* sp.	Leaf, Berry, Shoot	Tempranillo, Moscatel Grano Menudo, Malvar, Syrah, Merlot, Garnacha, Albillo, Airen, Cabernet Sauvignon; Güal; Flame, Autumn Royal, Sweet Scarlet	Europe, North America, Europe	Ascomycota	[84, 96, 109]
21.	*Aureobasidium pullulans*	Stem, Twig, Leaf	Midnight beauty, Tempranillo, Moscatel Grano Menudo, Malvar, Syrah, Merlot, Garnacha, Albillo, Airen, Cabernet Sauvignon; Chardonnay and Merlot; Albillo, Almuneco, Baboso Negro, Moscatel, Listan Negro, and Verdelho; Midnight	Asia; Africa; South America; Europe; Australia	Ascomycota	[64, 80, 96, 105, 123]
22.	*Aureobasidium* sp.	Leaf, Node, Internode	Tokai and Merlot	Europe	Ascomycota	[77]
23.	*Bipolaris cynodontis*	Leaf	*Vitis amurensis*	East Asia	Ascomycota	[102]
24.	*Bionectria ochroleuca*	Stem	Moscatel	Europe	Ascomycota	[123]
25.	*Bipolaris sorokiniana*	Stem	Midnight beauty	East Asia	Ascomycota	[80]

Table 1 (continued)

Sl. No	Fungal Endophyte	Host Part	Grape variety	Location	Division	References
26.	*Biscogniauxia mediterranea*	Leaf	L'Acadie blanc	North America	Ascomycota	[83]
27.	*Bjerkandera adusta*	Leaf, Root, Petiole, Offshoot	*V. labrusca* cv. 'Niagara Rosada'; Trincadeira and Alicante Bouschet	South America, Europe	Basidiomycota	[104, 105]
28.	*Botryosphaeria dothidea*	Stem	Midnight beauty	East Asia	Ascomycota	[80]
29.	*Botryosphaeria lutea*	Shoot	Verdelho	Europe	Ascomycota	[109]
30.	*Botryosphaeria obtuse*	Twig	Tempranillo, Moscatel Grano Menudo, Malvar, Syrah, Merlot, Garnacha, Albillo, Airen, Cabernet Sauvignon	Europe	Ascomycota	[96]
31.	*Botryosphaeria parva*	Bark, Stem	Moscatel, Tempranillo, and Verdelho; Albillo, Almuneco, Malvasia, Listan Blanco, Listan Negro, Torronte and Verdelho	Asia, Europe	Ascomycota	[109, 123]
32.	*Botryosphaeria ribis*	Stem	Listan Negro	Europe	Ascomycota	[123]
33.	*Botryosphaeria stevensii*	Leaf, Root, Twig	Tempranillo, Moscatel Grano Menudo, Malvar, Syrah, Merlot, Garnacha, Albillo, Airen, Cabernet Sauvignon;	Europe	Ascomycota	[96]
34.	*Botryotinia fuckeliana*	Stem	Chardonnay and Merlot	Europe	Ascomycota	[64]
35.	*Botrytis cinera*	Stem, Berry, Root, Offshoot	Midnight beauty; Flame, Autumn Royal, Sweet Scarlet; Trincadeira and Alicante Bouschet	East Asia, North America, Europe	Ascomycota	[80, 84, 104]
36.	*Chaetomium globosum*	Stem, Leaf, Twig, Shoot	Tempranillo, Moscatel Grano Menudo, Malvar, Syrah, Merlot, Garnacha, Albillo, Airen, Cabernet Sauvignon; Tempranillo; Midnight beauty	Europe, East Asia	Ascomycota	[80, 96, 109]
37.	*Chaetomium* sp.	Twig, Shoot, Root	Tempranillo, Moscatel Grano Menudo, Malvar, Syrah, Merlot, Garnacha, Albillo, Airen, Cabernet Sauvignon; Cabernet Sauvignon and Chardonnay	Europe, South America	Ascomycota	[96, 106]
38.	*Chaetomium succineum*	Root	Trincadeira and Alicante Bouschet	Europe	Ascomycota	[104]
39.	*Cladosporium cladosporioides*	Stem, Shoot	Negramoll, Listan negro; Midnight beauty	East Asia, Europe	Ascomycota	[80, 109]

Table 1 (continued)

Sl. No	Fungal Endophyte	Host Part	Grape variety	Location	Division	References
40.	*Cladosporium herbarum*	Leaf	Tempranillo, Moscatel Grano Menudo, Malvar, Syrah, Merlot, Garnacha, Albillo, Airen, Cabernet Sauvignon	Europe	Ascomycota	[96]
41.	*Cladosporium ramotenellum*	Stem	Midnight beauty	East Asia	Ascomycota	[80]
42.	*Cladosporium silenes*	Stem	Midnight beauty	East Asia	Ascomycota	[80]
43.	*Cladosporium* sp.	Shoot, Root, Sap, Cordon, Cane, Berry, Leaf, Node, Internode	Tokai and Merlot; Chardonnay and Merlot; Flame, Autumn Royal, and Sweet Scarlet; Cabernet Sauvignon and Chardonnay	North America, Europe, South America	Ascomycota	[64, 77, 84, 85, 106]
44.	*Cladosporium sphaerospermum*	Stem	Midnight beauty	East Asia	Ascomycota	[80]
45.	*Cladosporium tenellum*	Stem	Midnight beauty	East Asia	Ascomycota	[80]
46.	*Cladosporium tenuissimum*	Stem	Midnight beauty	East Asia	Ascomycota	[80]
47.	*Clonostachys rosea*	Shoot, Root, Offshoot	Trincadeira and Alicante Bouschet; Cabernet Sauvignon and Chardonnay	South America, Europe	Ascomycota	[104, 106]
48.	*Colletotrichum boninense*	Leaf	*V. labrusca* cv. 'Niagara Rosada'	South America	Basidiomycota	[105]
49.	*Colletotrichum gloesporioides*	Leaf	*V. labrusca* cv. 'Niagara Rosada'; Rose honey	Europe, South America	Ascomycota	[105, 117]
50.	*Colletrotrichum* sp.	Leaf, Root, Petiole	Tempranillo, Moscatel Grano Menudo, Malvar, Syrah, Merlot, Garnacha, Albillo, Airen, Cabernet Sauvignon; Trincadeira and Alicante Bouschet	Europe	Ascomycota	[96, 104]
51.	*Coprinellus* sp.	Leaf	L'Acadie blanc	North America	Basidiomycota	[83]
52.	*Curvularia americana*	Stem	Midnight beauty	East Asia	Ascomycota	[80]
53.	*Cylindrocarpon destructans*	Twig	Tempranillo, Moscatel Grano Menudo, Malvar, Syrah, Merlot, Garnacha, Albillo, Airen, Cabernet Sauvignon	Europe	Ascomycota	[96]
54.	*Cytospora acaceae*	Petiole, Offshoot	Trincadeira and Alicante Bouschet	Europe	Ascomycota	[104]
55.	*Davidiella tassiana*	Stem	Chardonnay and Merlot	Europe	Ascomycota	[64]
56.	*Diaporthe helianthi*	Leaf	*V. labrusca* cv. 'Niagara Rosada'	South America	Basidiomycota	[105]
57.	*Diaporthe* sp.	Root, Petiole, Offshoot	Trincadeira and Alicante Bouschet	Europe	Ascomycota	[104]

Table 1 (continued)

Sl. No	Fungal Endophyte	Host Part	Grape variety	Location	Division	References
58.	*Diaporthe phaseolorum*	Leaf	*V. labrusca* cv. 'Niagara Rosada'	South America	Basidiomycota	[105]
59.	*Diplodia pseudoseriata*	Offshoot	Trincadeira and Alicante Bouschet	Europe	Ascomycota	[104]
60.	*Epicoccum nigrum*	Leaf, Stem, Root, Petiole	Tempranillo, Moscatel Grano Menudo, Malvar, Syrah, Merlot, Garnacha, Albillo, Airen, Cabernet Sauvignon; *V. labrusca* cv. 'Niagara Rosada'; Chardonnay and Merlot; L'Acadie blanc; Cabernet Sauvignon; Cabernet Sauvignon and Chardonnay; Trincadeira and Alicante Bouschet	Europe, North America, South America, East Asia, Europe	Ascomycota	[64, 83, 96, 104–106, 117]
61.	*Epicoccum*	Leaf, Node, Internode	Tokai and Merlot	Europe	Ascomycota	[77]
62.	*Eupenicillium* sp.	Root	Trincadeira and Alicante Bouschet	Europe	Ascomycota	[104]
63.	*Eutypa* sp.	Stem	Malvasia Lanzarote	Europe	Ascomycota	[123]
64.	*Flavodon flavus*	Leaf	*V. labrusca* cv. 'Niagara Rosada'	South America	Basidiomycota	[105]
65.	*Fusarium acuminatum*	Leaf	*V. labrusca* cv. 'Niagara Rosada'	South America	Ascomycota	[105]
66.	*Fusarium oxysporum*	Leaf, Root, Petiole, Offshoot	Cabernet Sauvignon; Trincadeira and Alicante Bouschet	East Asia, Europe	Ascomycota	[104, 117]
67.	*Fusarium proliferatum*	Twig	Tempranillo, Moscatel Grano Menudo, Malvar, Syrah, Merlot, Garnacha, Albillo, Airen, Cabernet Sauvignon	Europe	Ascomycota	[96]
68.	*Fusarium sacchari*	Leaf	*V. labrusca* cv. 'Niagara Rosada'	South America	Ascomycota	[105]
69.	*Fusarium subglutinans*	Leaf	*V. labrusca* cv. 'Niagara Rosada'	South America	Ascomycota	[105]
70.	*Fusarium verticillioides*	Root, Offshoot	Trincadeira and Alicante Bouschet	Europe	Ascomycota	[104]
71.	*Geotrichum* sp.	Leaf	Tempranillo, Moscatel Grano Menudo, Malvar, Syrah, Merlot, Garnacha, Albillo, Airen, Cabernet Sauvignon	Europe	Ascomycota	[96]

Table 1 (continued)

Sl. No	Fungal Endophyte	Host Part	Grape variety	Location	Division	References
72.	*Gibberella avenacea*	Twig	Tempranillo, Moscatel Grano Menudo, Malvar, Syrah, Merlot, Garnacha, Albillo, Airen, Cabernet Sauvignon	Europe	Ascomycota	[96]
73.	*Gibberella intricans*	Shoot	Tempranillo	Europe	Ascomycota	[109]
74.	*Gibberella pulicaris*	Shoot, Stem	Chardonnay and Merlot	Europe	Ascomycota	[64]
75.	*Guignardia mangiferae*	Leaf	*V. labrusca* cv. 'Niagara Rosada'	South America	Basidiomycota	[105]
76.	*Hormonema viticola*	Root, Petiole, Offshoot	Trincadeira and Alicante Bouschet	Europe	Ascomycota	[104]
77.	*Hortaea werneckii*	Shoot	Negramoll	Europe	Ascomycota	[109]
78.	*Humicola* sp.	Twig	Tempranillo, Moscatel Grano Menudo, Malvar, Syrah, Merlot, Garnacha, Albillo, Airen, Cabernet Sauvignon;	Europe	Ascomycota	[96]
79.	*Hypoxylon fragiforme*	Leaf	L'Acadie blanc	North America	Ascomycota	[83]
80.	*Hypoxylon lateripigmentum*	Stem	Midnight beauty	East Asia	Ascomycota	[80]
81.	*Hypoxylon serpens*	Twig	Tempranillo, Moscatel Grano Menudo, Malvar, Syrah, Merlot, Garnacha, Albillo, Airen, Cabernet Sauvignon	Europe	Ascomycota	[96]
82.	*Hypoxylon* sp.	Leaf	L'Acadie blanc	North America	Ascomycota	[83]
83.	*Irpex lacteus*	Leaf	L'Acadie blanc	North America	Basidiomycota	[83]
84.	*Kalmusia variispora*	Berry	Flame, Autumn Royal, Sweet Scarlet	North America	Ascomycota	[84]
85.	*Lasiodiplodia theobromae*	Stem	Midnight beauty	East Asia	Ascomycota	[80]
86.	*Lecythophora hoffmannii*	Leaf	L'Acadie blanc	North America	Ascomycota	[83]
87.	*Lenzites elegans*	Leaf	*V. labrusca* cv. 'Niagara Rosada'	South America	Basidiomycota	[105]
88.	*Leptosphaeria* sp.	Leaf	Tempranillo, Moscatel Grano Menudo, Malvar, Syrah, Merlot, Garnacha, Albillo, Airen, Cabernet Sauvignon; Trincadeira and Alicante Bouschet	Europe	Ascomycota	[96, 104]
89.	*Leptosphaerulina chartarum*	Stem	Chardonnay and Merlot	Europe	Ascomycota	[64]
90.	*Libertella* sp.	Leaf	Tempranillo, Moscatel Grano Menudo, Malvar, Syrah, Merlot, Garnacha, Albillo, Airen, Cabernet Sauvignon	Europe	Ascomycota	[96]

Table 1 (continued)

Sl. No	Fungal Endophyte	Host Part	Grape variety	Location	Division	References
91.	*Macrophomina phaseolina*	Leaf, Root, Petiole, Offshoot	Tempranillo, Moscatel Grano Menudo, Malvar, Syrah, Merlot, Garnacha, Albillo, Airen, Cabernet Sauvignon	Europe	Ascomycota	[96]
92.	*Mucor hiemalis*	Stem, Leaf	Tempranillo, Moscatel Grano Menudo, Malvar, Syrah, Merlot, Garnacha, Albillo, Airen, Cabernet Sauvignon;	Europe	Mucoromycota	[96]
93.	*Mucor* sp.	Leaf	Tempranillo, Moscatel Grano Menudo, Malvar, Syrah, Merlot, Garnacha, Albillo, Airen, Cabernet Sauvignon;	Europe	Mucoromycota	[96]
94.	*Mycosphaerella graminicola*	Stem	Midnight beauty	East Asia	Ascomycota	[80]
	Nectria fuckeliana	Twig	Tempranillo, Moscatel Grano Menudo, Malvar, Syrah, Merlot, Garnacha, Albillo, Airen, Cabernet Sauvignon	Europe	Ascomycota	[96]
	Nectria ramulariae	Twig	Tempranillo, Moscatel Grano Menudo, Malvar, Syrah, Merlot, Garnacha, Albillo, Airen, Cabernet Sauvignon	Europe	Ascomycota	[96]
	Neofusicoccum parvam	Stem, Root, Petiole, Offshoot	Chardonnay and Merlot; Trincadeira and Alicante Bouschet	Europe	Ascomycota	[64, 104]
	Nigrospora oryzae	Stem	Midnight beauty	East Asia	Ascomycota	[80]
	Nigrospora sp.	Leaf	Rose honey	Europe	Ascomycota	[117]
	Nigrospora sphaerica	Stem, Leaf	Midnight beauty; Rose honey	East Asia	Ascomycota	[80, 117]
	Nodulisporium sp.	Leaf	Tempranillo, Moscatel Grano Menudo, Malvar, Syrah, Merlot, Garnacha, Albillo, Airen, Cabernet Sauvignon	Europe	Ascomycota	[96]
	Ophiostoma piceae	Twig	Tempranillo, Moscatel Grano Menudo, Malvar, Syrah, Merlot, Garnacha, Albillo, Airen, Cabernet Sauvignon	Europe	Ascomycota	[96]
	Paraconiothyrium variabile	Leaf	L'Acadie blanc	North America	Ascomycota	[83]
	Paraphaeosphaeria pilleata	Leaf	*V. labrusca* cv. 'Niagara Rosada'	South America	Basidiomycota	[104]
	Penicillium digitatum	Stem	Midnight beauty	East Asia	Ascomycota	[80]
	Penicillium glabrum	Root, Petiole, Offshoot	Trincadeira and Alicante Bouschet	Europe	Ascomycota	[103]
	Penicillium solitum	Stem	Tintilla	Europe	Ascomycota	[123]

Table 1 (continued)

Sl. No	Fungal Endophyte	Host Part	Grape variety	Location	Division	References
	Penicillium sp.	Leaf, Shoot, Root, Petiole, Offshoot	Tempranillo, Moscatel Grano Menudo, Malvar, Syrah, Merlot, Garnacha, Albillo, Airen, Cabernet Sauvignon; Negramoll; L'Acadie blanc; Trincadeira and Alicante Bouschet	Europe, North America	Ascomycota	[83, 96, 104, 109]
	Penicillium thomii	Root, Petiole, Offshoot	Trincadeira and Alicante Bouschet	Europe	Ascomycota	[104]
	Pestalotia sp.	Leaf, Node, Internode	Tokai and Merlot	Europe	Ascomycota	[77]
	Pestalotiopsis sp.	Shoot, Leaf, Node, Internode, Offshoot	Tokai and Merlot; Verdelho and Terrantes; Trincadeira and Alicante Bouschet	Europe	Ascomycota	[104, 77, 109]
	Peyronellaea pinodella	Leaf	L'Acadie blanc	North America	Ascomycota	[83]
	Phaeoacremonium aleophilum	Twig	Tempranillo, Moscatel Grano Menudo, Malvar, Syrah, Merlot, Garnacha, Albillo, Airen, Cabernet Sauvignon	Europe	Ascomycota	[96]
	Phaeoacremonium inflatipes	Twig	Tempranillo, Moscatel Grano Menudo, Malvar, Syrah, Merlot, Garnacha, Albillo, Airen, Cabernet Sauvignon;	Europe	Ascomycota	[96]
	Phaeomoniella chlamydospora	Twig	Tempranillo, Moscatel Grano Menudo, Malvar, Syrah, Merlot, Garnacha, Albillo, Airen, Cabernet Sauvignon	Europe	Ascomycota	[96]
	Phanerochaete sordida	Leaf	*V. labrusca* cv. 'Niagara Rosada'	South America	Basidiomycota	[105]
	Phialophora fastigiata	Root	Trincadeira and Alicante Bouschet	Europe	Ascomycota	[104]
	Phialophora sp.	Leaf, Root, Petiole, Offshoot	Tempranillo, Moscatel Grano Menudo, Malvar, Syrah, Merlot, Garnacha, Albillo, Airen, Cabernet Sauvignon; Trincadeira and Alicante Bouschet	Europe	Ascomycota	[96, 104]
	Phoma aliena	Leaf	L'Acadie blanc	North America	Ascomycota	[83]
	Phoma glomerata	Twig, Leaf	Tempranillo, Moscatel Grano Menudo, Malvar, Syrah, Merlot, Garnacha, Albillo, Airen, Cabernet Sauvignon;	Europe	Ascomycota	[96]

Table 1 (continued)

Sl. No	Fungal Endophyte	Host Part	Grape variety	Location	Division	References
	Phoma herbarum	Stem	Chardonnay and Merlot; Midnight beauty	East Asia	Ascomycota	[64, 80]
	Phoma medicaginis	Stem	Albillo and Listan Blanco	Europe	Ascomycota	[123]
	Phoma sp.	Twig, Leaf, Node, Internode	Tokai and Merlot; Tempranillo, Moscatel Grano Menudo, Malvar, Syrah, Merlot, Garnacha, Albillo, Airen, Cabernet Sauvignon; L'Acadie blanc; *Vitis amurensis*	Europe, North America, East Asia	Ascomycota	[77, 83, 96, 102]
	Phomopsis viticola	Twig	Tempranillo, Moscatel Grano Menudo, Malvar, Syrah, Merlot, Garnacha, Albillo, Airen, Cabernet Sauvignon	Europe	Ascomycota	[96]
	Phyllosticta sp.	Leaf	*V. labrusca* cv. 'Niagara Rosada'	South America	Basidiomycota	[105]
	Purpureocillium lilacinum	Shoot, Root	Cabernet Sauvignon and Chardonnay	South America	Ascomycota	[106]
	Pleurotus nebrodensis	Leaf	*V. labrusca* cv. 'Niagara Rosada'	South America	Basidiomycota	[105]
	Preussia africana	Leaf	*V. labrusca* cv. 'Niagara Rosada'	South America	Basidiomycota	[105]
	Ramularia pratensis	Leaf	L'Acadie blanc	North America	Ascomycota	[83]
	Ramularia sp.	Leaf	L'Acadie blanc	North America	Ascomycota	[83]
	Rhinocladiella atrovirens	Twig	Tempranillo, Moscatel Grano Menudo, Malvar, Syrah, Merlot, Garnacha, Albillo, Airen, Cabernet Sauvignon	Europe	Ascomycota	[96]
	Rhizoctonia solani	Twig	Tempranillo, Moscatel Grano Menudo, Malvar, Syrah, Merlot, Garnacha, Albillo, Airen, Cabernet Sauvignon;	Europe	Basidiomycota	[96]
	Rhizopus stolonifer	Leaf	Tempranillo, Moscatel Grano Menudo, Malvar, Syrah, Merlot, Garnacha, Albillo, Airen, Cabernet Sauvignon;	Europe	Zygomycota	[96]
	Rhizosphaera sp.	Leaf	L'Acadie blanc	North America	Ascomycota	[83]
	Rutstroemiaceae sp.	Root, Petiole, Offshoot	Trincadeira and Alicante Bouschet	Europe	Ascomycota	[103]

Table 1 (continued)

Sl. No	Fungal Endophyte	Host Part	Grape variety	Location	Division	References
	Sclerotinia Sclerotiorum	Leaf, Trunk	Tempranillo, Moscatel Grano Menudo, Malvar, Syrah, Merlot, Garnacha, Albillo, Airen, Cabernet Sauvignon	Europe	Ascomycota	[96]
	Scopulariopsis brevicaulis	Stem	Midnight beauty	East Asia	Ascomycota	[80]
	Selenophoma sp.	Leaf	Tempranillo, Moscatel Grano Menudo, Malvar, Syrah, Merlot, Garnacha, Albillo, Airen, Cabernet Sauvignon	Europe	Ascomycota	[96]
	Slerotinia scleratiorum	Twig	Tempranillo, Moscatel Grano Menudo, Malvar, Syrah, Merlot, Garnacha, Albillo, Airen, Cabernet Sauvignon	Europe	Ascomycota	[96]
	Sordaria sp.	Twig	Tempranillo, Moscatel Grano Menudo, Malvar, Syrah, Merlot, Garnacha, Albillo, Airen, Cabernet Sauvignon	Europe	Ascomycota	[96]
	Sporormiella intermedia	Twig	Tempranillo, Moscatel Grano Menudo, Malvar, Syrah, Merlot, Garnacha, Albillo, Airen, Cabernet Sauvignon	Europe	Ascomycota	[96]
	Stemphylium sp.	Leaf	Tempranillo, Moscatel Grano Menudo, Malvar, Syrah, Merlot, Garnacha, Albillo, Airen, Cabernet Sauvigno	Europe	Ascomycota	[96]
	Talaromyces sp.	Root, Petiole, Offshoot	Trincadeira and Alicante Bouschet	Europe	Ascomycota	[103]
	Tinctoporellus epimiltinus	Leaf	*V. labrusca* cv. 'Niagara Rosada'	South America	Basidiomycota	[104]
	Torula sp.	Leaf	Tempranillo, Moscatel Grano Menudo, Malvar, Syrah, Merlot, Garnacha, Albillo, Airen, Cabernet Sauvignon	Europe	Ascomycota	[96]
	Trichothecium roseum	Leaf	Rose honey	East Asia	Ascomycota	[117]
	Trichothecium sp.	Leaf, Root, Petiole, Offshoot	Rose honey; Trincadeira and Alicante Bouschet	East Asia, Europe	Ascomycota	[104, 117]
	Truncatella angustata	Twig, Stem, Root	Tempranillo, Moscatel Grano Menudo, Malvar, Syrah, Merlot, Garnacha, Albillo, Airen, Cabernet Sauvignon; Chardonnay and Merlot; Trincadeira and Alicante Bouschet	Europe	Ascomycota	[64, 96, 104]

Table 1 (continued)

Sl. No	Fungal Endophyte	Host Part	Grape variety	Location	Division	References
	Ulocladium sp.	Leaf	Tempranillo, Moscatel Grano Menudo, Malvar, Syrah, Merlot, Garnacha, Albillo, Airen, Cabernet Sauvignon	Europe	Ascomycota	[96]
	Xylaria berteri	Leaf	*V. labrusca* cv. 'Niagara Rosada'	South America	Ascomycota	[105]
	Xylaria hypoxylon	Twig	Tempranillo, Moscatel Grano Menudo, Malvar, Syrah, Merlot, Garnacha, Albillo, Airen, Cabernet Sauvignon	Europe	Ascomycota	[96]
	Xylaria sp.	Stem	Chardonnay and Merlot	Europe	Ascomycota	[64]

prior to taxonomic identification based on macroscopic and microscopic observations. Non-culturable FEs are characterized directly by grinding fungal tissues and extracting total genomic DNA for identification using Denaturing Gradient Gel Electrophoresis (DGGE) [77], Automated Ribosomal Intergenic Spacer Analysis (ARISA) [64], Random Amplified Polymorphic DNA (RAPD) [78], Single-Strand Conformation Polymorphism (SSCP) analysis [79], and through Next-Generation Sequencing (NGS) technologies [80] (Fig. 4). Several different studies of the FEs community in the grapevine organs have been published. Among them stem, berries, seeds and leaves showed greater diversity as compared with other explants. The leaves showed the maximum richness of endophytes in both culture-dependent and culture-independent molecular approaches [76]. A similar study showed that different ages viz., 3, 8 and 13-years-old stems of *V. vinifera* cv. Midnight when compared, concluded to have more culturable diversity in the 13-year-old stem than 3-year and 8-year-old stems [80]. Another study revealed the community of FEs between young and old age branches [81]. Taxa obtained from 3 to 8-year-old branches were three times higher than younger age groups. Abundance of cultured fungi was found similar for all ages except for 2 and 10-month-old branches. A community of specific FEs were found to harbour grapevine wood and were age independent. Significant differences were observed between 2-year-old and 10 months old as well as between 2-year-old and 3-year-old, due to the low number of species isolated from 2-year-old branches [81]. From healthy, recovered, and phytoplasma-infected grapevines, non-culturable FEs were characterized using DGGE analysis [77]. Fungal endophytic communities in grapevines of organic and integrated pest management practices, ARISA technique was used to demonstrate the major difference in their diversity profile [64]. Dissanayake et al. [80] studied non-culturable fungal richness of 59 operational taxonomic units (OTU) in 13-year-old grapevines followed by eight and three years. Most of the short sequence fragments of ITS region targeted by NGS for fungal community investigations was found to be insufficient for species-level identification at the accepted threshold level of 97% sequence similarity for endophytic fungi [82]. Use of NGS data to identify the taxa in a community is not accurate at the species level, as compared to the analyses using multigene sequence data using cultures from the culture-dependent method [80]. Use of pyrosequencing has generated 1,34,712 distinct fungal sequences [83]. Recently, metagenomics through Illumina based on ITS sequence information, identified the distinct FEs patterns in three table grape varieties collected from the market viz., Flame (48,369 fungal OTUs), Autumn Royal (31,518 fungal OTUs), and Sweet Scarlet (6376 fungal OTUs) [Wijekoon and Quill 2021] [84].

Table 2 Geographical distribution of endophytic *Trichoderma* and *Beauveria* species originating from grapevines genotypes worldwide

Trichoderma species	Host Part	Grape variety	Location	Division	References
Trichoderma afroharzianum	Cordon	Furmint	Europe	Ascomycota	[110]
Trichoderma aggressivum	Shoot	Chardonnay and Merlot	Europe	Ascomycota	[64]
Trichoderma atrobrunneum	Cordon	Furmint	Europe	Ascomycota	[110]
Trichoderma aureoviride	Twig, Leaf	Tempranillo, Moscatel Grano Menudo, Malvar, Syrah, Merlot, Garnacha, Albillo, Airen, Cabernet Sauvignon	Europe	Ascomycota	[96]
Trichoderma gamsii	Cordon	Furmint	Europe	Ascomycota	[110]
Trichoderma harzianum	Twig, Leaf, Cordon	Tempranillo, Moscatel Grano Menudo, Malvar, Syrah, Merlot, Garnacha, Albillo, Airen, Cabernet Sauvignon	Europe	Ascomycota	[96, 110]
Trichoderma orientale	Cordon	Furmint	Europe	Ascomycota	[110]
Trichoderma reesei	Shoot	Chardonnay and Merlot	Europe	Ascomycota	[64]
Trichoderma simmonsii	Cordon	Furmint	Europe	Ascomycota	[110]
Trichoderma sp.	Twig, Leaf, Trunk	Tempranillo, Moscatel Grano Menudo, Malvar, Syrah, Merlot, Garnacha, Albillo, Airen, Cabernet Sauvignon; Tempranillo	Europe	Ascomycota	[96, 99]
Trichoderma altair	Shoot, Root	Cabernet Sauvignon and Chardonnay	South America	Ascomycota	[106]
Trichoderma virens	Shoot	Chardonnay and Merlot	East Asia	Ascomycota	[64]
Beauveria bassiana	Bud, Root, Petiole	Riesling; Trincadeira and Alicante Bouschet, Taify	Europe; Asia	Ascomycota	[103, 104]

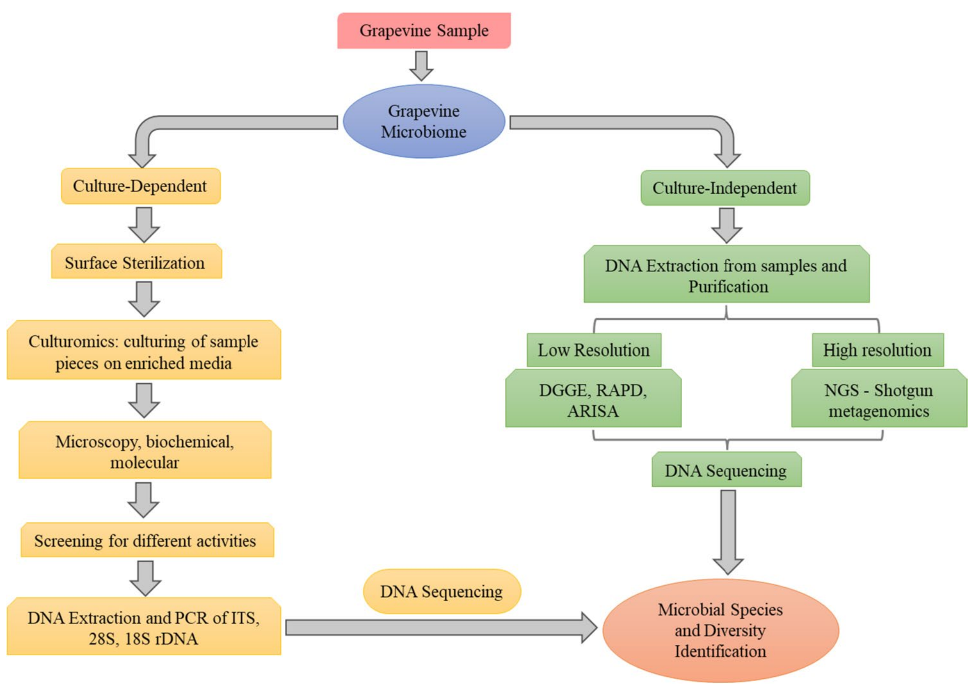

Fig. 4 Schematic representation of the major steps for identification of culture-dependent and culture-independent fungal endophytes from plants

The diversity and richness of FEs may show seasonal variation. Study of fungal endophyte strains were rich in autumn than in summer with a total of 11 genera in common. In addition, a comparative study between different cultivars of *Vitis amurensis* and *Vitis vinifera* showed that the minimum share was governed by a common class of Dothideomycetes followed by the class Tremellomycetes in both the cultivars [76, 85]. A study on endophytic *Acremonium byssoides* which was isolated during different months and seasons from *V. vinifera* cv. Regina Bianca (table grape variety), cv. Catarratto, and cv. Insolia (wine grape varieties). Result stated that the higher diversity of FEs was obtained during cooler months for cv. Catarratto and cv. Insolia and in summer months for cv. Regina Bianca [15]. During moist and cool periods, buds and shoots are better sources of endophyte isolation. In autumn collected samples, FEs seemed to be regularly isolated but due to adverse environmental conditions, the nutrient in leaves decreased and impacted the microenvironment in which *Acremonium. byssoides* developed [15].

The diversity of endophytic fungi alters between wild and hybrid *Vitis* due to being genetically distinct and grown for specific traits [86]. Another important factor responsible for endophytic population structure is growing wild plants share endophytes from other plants [87]. A study between wild cultivar, *V. riparia,* and hybrid cultivar Acadie Blanc, which was grown in conventional and organic management conditions observed high species richness and diversity of FEs in the wild vines than the hybrid species. In addition, wild *Vitis* genotypes are in close vicinity of the main cultivars which have been shown to have rare and unidentified endophytes [83]. Similarly, Fan et al. [88], correlated the fungal endophytic community have rich diversity in young leaves than in mature leaves of both the cultivars. In addition, wild grapevine (*V. amurensis* cv. Shaungyou) showed to have a high diversity of FEs than cultivated grapevine (*V. vinifera* cv. Red Globe). Recently, In India, 51 FEs were isolated from the leaves of 10 different juice, wine, table varieties, and a wild genotype, which showed maximum diversity in table varieties when compared to others, while, few FEs were found common in all genotypes [28].

Application of fungicides on plants may fluctuate the composition of endophytes but their endurance among fungi is unexplored [64]. For example, species diversity in the conventional vineyard which was subjected to fungicide was low as compared to organic vineyards which were at the intermediate level [83]. Conversely, a study of different cultivars grown in conventional and biological modes showed high endophyte microbial diversity in the conventional mode [89]. Similarly, an approach with multivariate analysis of cultivable fungi and DNA-based study revealed that a community of FEs under integrated pest management and organic vineyard are significantly distinct, and due to long-term use of fungicides, the composition is also impacted in IPM [64].

Interaction of Fungal Endophyte with Phytopathogen

Synthetic chemical fungicides and pesticides have become common in agriculture for disease prevention [90]. The widespread use of these pesticides has adversely affected mutualistic microbiomes and drastically reduced crop health [90]. FEs act as potential BCA to produce antibacterial and antifungal compounds which could be an alternative to these active compounds [91]. These BCAs are eco-friendly and reduce pathogen retention while benefitting the crops. These approaches are becoming more popular and have not yet been investigated intensively, but they possess the potential for crop protection [92–95]. Literatures have shown that FEs isolated from grapevines have pathogen defense mechanisms including induced systemic resistance (ISR), accumulation of pathogenesis-related (PR) proteins, expression of plant defense genes, production of secondary metabolites, and competition with pathogens for ecological niches in terms of nutrients and space availability [65, 96]. Owing to several factors, including competition for space within the host plant and/or the synthesis of antimicrobial substances such as stilbenes, the antipathogenic properties of grapevine FEs have drawn substantial interest [97–99]. The FEs isolated from grapes have controlled various grapevine phytopathogens using several mechanisms listed in Table 3.

FEs cultured from various parts of the grapevine are being studied to control major grapevine diseases. FEs *Acremonium* sp. strain A20 isolated from leaves of the grapevine showed significant activity against *Plasmopara viticola* [100]. BCAs crude extract inhibited the germination of *P. viticola* sporangia, which was further assessed. They produce six novel metabolites named acremines which showed the capability of decreasing germination [100]. Similarly, *A. byssoides* isolated from the leaves of cv. Regina Bianca parasitized *P. viticola* and the same endophyte obtained from different cultivars of Insolia has different mechanisms which completely inhibited *P. viticola* using culture filtrate [15]. Burruano et al. [15] isolated *A. persicinum* from leaves of cv. Regina Bianca was further used to investigate its inhibitory activity conducted by Lo Piccolo et al. [78]. This fungal endophyte exploited an antibiosis mechanism to impede sporangia germination of *P. viticola*.

Taxa from the *Alternaria* group have been characterized as endophytes of grapes [101]. In the study by Musetti et al. [17], *A. alternata* was isolated from the leaves of abandoned grapevine in Italy and reported to inhibit *P. viticola* on grapevine leaves under laboratory conditions. Further, this endophyte produced secondary metabolite diketopiperazines which was tested on leaf discs and in the greenhouse were particularly efficient in suppressing the sporulation of *P. viticola* [17]. *Albifimbria verrucaria*, a potential BCA has been reported to control grey mould caused by *Botrytis cinerea*. The mycelial growth and conidium germination of *B. cinerea* were shown to have been greatly reduced in an in vitro study employing a culture extract of *A. verrucaria*. Also, this endophyte produces chitinase enzyme might be another mechanism responsible for the degradation of conidia and mycelia of the pathogen [102]. Moreover, using *A. verrucaria* culture extracts against *B. cinerea* reduced incidence considerably and drastically reduced disease severity [102]. The most common FE *Beauveria bassiana* was isolated from the leaves of *Vitis vinifera* cv. Taify and checked its efficacy against *Aphis illinoisensis* [103]. The

Table 3 Various antagonistic mechanisms by fungal endophytes used against grapevine phytopathogen

Grapevine pathogen	Fungal endophyte	Mode of Inhibition	References
Botrytis cinerea (Grey mould)	*Albifimbria verrucaria*	Secondary metabolite, lytic enzyme	[102]
	Penicillium sp.	Secondary metabolite	[109]
Plasmopara viticola (Downy mildew)	*Acremonium byssoides*	Mycoparasitism, secondary metabolite	[15]
	Acremonium persicinum	Antibiosis	[78]
	Acremonium sp.	Secondary metabolite	[100]
	Alternaria alternata	Secondary metabolite	[16, 17]
	Epicoccum nigrum	Secondary metabolite	[56, 107]
	Fusarium proliferatum	Mycoparasitism	[16, 108]
	Fusarium proliferatum	Mycoparasitism, lytic enzyme	[20]
Fusarium oxysporum f.sp. *herbenontis* (wilt disease)	*Colletotrichum gloeosporioides*	Competition	[105]
	Flavodon flavus	Competition	[105]
Grapevine Trunk disease (GTD)	*Aspergillus niger*	Competition or secondary metabolite	[104]
	Clonostachys rosea	Antibiosis	[106]
	Fusarium oxysporum	Competition	[103]
	Trichoderma sp.	Mycoparasitism and Competition	[99]
	T. afroharzianum	Mycoparasitism	[110]
	T. simmonsii	Mycoparasitism	[110]
Other grapevine pathogens or postharvest pathogens	*Aureobasidium pullulans*	Competition	[56, 96]

two endophytic isolates of *B. bassiana* under test showed a difference in virulence between them, with the Bb-Taif1 isolate showing greater virulence than the Bb-Taif2 isolate] [103].

Aspergillus niger has been reported to directly inhibit the growth of fungal pathogens *Diaporthe* sp., *D. pseudoseriata* and *Phialophora fastigiata* which are responsible for the development of Grapevine Trunk Disease (GTD) in grapevine. In this study, *A. niger* inhibited pathogen growth through competition or by the production of metabolites [104]. Three different species viz., *A. flavus*, *A. niger*, and *A. oryzae* were able to inhibit *C. gloeosporioides* under *in-vitro* dual culture plate assay either due to competition or antibiosis [28]. In similar study, *Curvularia lunata*, *C. verruculosa*, *Daldinia eschscholtzii,* and *Aspergillus nomiae* were evaluated in inverted plate assay, where these FEs produced volatile organic compounds (VOCs) responsible for inhibition of *C. gloeosporioides* [28]. Reported BCA i.e., *A. pullulans* has numerous mechanisms viz., competition for nutrients and space, production of pectolytic enzymes, polysaccharides, or antimicrobial metabolites [56, 96]. *Colletotrichum gloeosporioides* is known as grapevine pathogen causing anthracnose disease in India but in the study, it was identified as an endophyte and showed antagonistic behaviour towards *F. oxysporum* f. sp. *herbemontis* [105]. Strains of *Clonostachys rosea* were able to inhibit the growth of three pathogens viz., *D. seriata*, *Neofusicoccum parvum,* and *P. chlamydospora* causing GTD. The growth of pathogens was terminated before the interaction in correspondence with the zone of inhibition surrounding the antagonist, which indicated secretion of the antibiotic compound. After direct contact between *C. rosea* and the test pathogen, hyphal coiling was observed, which is a sign of mycoparasitism [106].

Epicoccum nigrum was identified as an important BCA which have been reported to have antagonistic activity on various grapevine pathogens. Martini et al. [56] examined the potential role of *E. nigrum*, due to its ability to produce secondary metabolite with antibiosis and this product was commercially developed. *Epicoccum nigrum* inhibits the growth of *P. viticola* [107]. An *in-vitro* preliminary assay was performed against several grapevine pathogens, *E. nigrum* isolates were able to inhibit *Phaeomoniella chlamydospore*, causing Petri disease known for decline in young vines [96].

Flavodun flavus is a FE isolated from the leaves of cv. Niagara Rosada has high antagonistic activity against *F. oxysporum f.* sp *herbemontis* [105]. Application of *Fusarium proliferatum* after downy mildew infection resulted in a reduction in spore production and prevention of re-sporulation [108]. Microscopic examination of the mechanism showed hyphal interaction, *F. proliferatum* hyphae coiling around and inside sporangiophores of *P. viticola* resulting in a mycoparasitism. Two susceptible *Vitis* interspecific hybrids received *F. proliferatum* treatments four-year, which significantly reduced the severity of infection [20], mutated *F. proliferatum* was first used in the study conducted by Falk et al. [108], producing a cold-tolerant strain that could regulate *P. viticola* on grapevine leaves in *in-vitro* conditions. Another antagonistic activity was studied against phytopathogens responsible for grapevine trunk disease (GTD), whereas, *F. oxysporum* showed the highest percentage of inhibition which revealing that competition might be a possible mechanism [104].

In vitro bioassays of endophytic fungi *Penicillium* sp. against *B. cinerea* showed a zone of inhibition at the point of interaction resulting in high antagonistic activity [109]. *Trichoderma* sp. isolated from wood of cv. Tempranillo was able to successfully colonize the plants and reduce the colonization of *Phaeoacremonium minimum*, a pioneer fungus involved in GTD and observed mechanisms were spore adhesion, niche exclusion, and mycoparasitism [99]. Another study revealed that *Trichoderma* isolates had similar activity against GTD pathogens. Strain TR04 *T. afroharzianum* and TR05 *T. simmonsii* were observed to have mycoparasitic activity against pathogens viz., *Diplodia seriata*, *Eutypa lata* and *Neofusicoccum parvum* [110].

Development in Growth and Quality of Grapevine

FEs can trigger plant defense mechanisms under biotic pressures. They involve the induction of genes that lead to production of defensive compounds that protect plants from pests, and diseases, and abiotic stresses viz., drought, high salinity, and low temperatures. Additionally, the interaction between host and FEs have been found benefitting plant growth and development. Furthermore, during the symbiosis, host, and endophyte metabolisms are interlinked through the exchange of compounds necessary for proper metabolic function [111]. The development and morphology of the host solely depend on the activity of the endophyte during interaction [112]. Endophytic symbioses have been observed to increase plant vigour, growth, and nutrient uptake capability [113–115]. In leaf and berry tissues [116], demonstrated eight isolated FEs (*Xylaria* sp., *Nigrospora* sp., *Chaetomium* sp., *Alternaria* sp., *Fusarium* sp., *Colletotrichum* sp., *Alternaria* sp., *Gibberella* sp.,) from the *Vitis vinifera* species responsible to change the levels of reducing sugar, total flavonoids, total phenols, trans-resveratrol, and phenylalanine ammonia-lyase activities. The inoculation of these FEs altered the physio-chemical condition of field-grown grapevines in both the leaves and berries during the ripening period. Additionally, due to the higher promoting effects of fungal endophyte strains such as CXB-11 (*Nigrospora* sp.) and CXC-13 (*Fusarium* sp.) on grapevine metabolites, distinct grape metabolite statuses were formed by their inoculation [116]. According to Huang et al. [117], grapevine flesh cells containing different endophytic fungi had different metabolite compositions, and they were strain/species-specific. This concludes that induced metabolites in the host due to interaction with FE can be used to improve grape qualities and characteristics.

Endophytes can produce secondary metabolites on their own, in addition, take part in the synthesis of secondary metabolites produced by plants [118, 119]. Resveratrol in grapes is a polyphenolic flavonoid naturally produced as a secondary metabolite and formed as a phytoalexin in reaction to stop an infection of *Botrytis cinerea* [98]. In China, Liu et al. [120] studied endophytic micro-organisms isolated from grapevine cv. Cabernet Sauvignon for their ability to produce resveratrol *in-vitro*, among them 36 FEs strains were assessed. The C2J6 strain of *Aspergillus niger*, which exhibits stable high resveratrol synthesis. Similarly, Dwibedi and Saxena [98] isolated 53 FEs with resveratrol-producing potential from different varieties of *V. vinifera* found in various parts of India. Identification of these FE is classified into seven genera- *Aspergillus*, *Botryosphaeria*, *Penicillium*, *Fusarium*, *Alternaria*, *Arcopilus*, and *Lasiodiplodia*.

Mantzoukas et al. [27] studied FE *Beauveria bassiana* showing effective colonization and enhancing the root development of *V. vinifera*. *Trichoderma* strains isolated from white grape cultivars from the Tokaj Wine Region in the northeastern part of Hungary were able to colonize Blaufraenkisch, Cabernet Franc, and Cabernet Sauvignon cultivars for up to four years after the treatment [121]. Furthermore, the bio-stimulatory impact resulted in increased burst vigour and acceleration of bud and shoot development, and increased sugar content in harvested grapes in *Trichoderma*-treated plants [121].

Conclusion

Utilization of potential FEs for management of grapevine diseases has been found most promising eco-friendly approach for sustainable and quality grape production worldwide. Much more research on FEs for managing bacterial and fungal diseases has been accomplished, but scanty information is available in India for managing grapevine diseases. The diversity of FEs originated from grapevine have been found based on type of genotype, tissues, age of explants and distinct geographical locations. These FEs having multifaceted effects like plant growth promotion, ISR to pests and diseases, nutrient-solubilizing ability, and improvement in yield and yield-contributing parameters. The FEs have significant potential of producing phytohormones, phosphate solubilization, siderophore synthesis, preventing plant diseases, and thereby promoting plant growth. For exploring the non-culturable EFs, novel techniques such as DGGE, ARISA, RAPD, SSCP and NGS are essential. Moreover, culturing the non-culturable FEs is a major challenge, nevertheless developing suitable media would certainly enhance isolation frequency. Fungal endophyte-host–pathogen interaction studies based on advanced microscopic techniques found useful in finding the movement of FEs in healthy and diseased plants. Development of formulations for field evaluation of potential FEs against major grapevine diseases is again a grey area of research. Therefore, FEs research need to be focussed more on their field evaluations at different geographical locations for residue degradation, diseases and pest management. For promoting, mass-scale production, commercial availability of FEs for their multifaceted benefits in the grapevine, Public–Private-Partnership is the only way-out to reach grape-growers for enhanced quality, export, residue compliance and for safe domestic consumption.

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Declarations

Conflict of interest All the authors declare that there is no potential conflict of interest.

Research Involving Human Participants and Animals In the present study no humans or animals were used.

Informed Consent No humans or animals were used in the present study.

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